

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Trait-modulated decline of carabid beetle occurrence along elevational gradients across the European Alps

This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1736947> since 2020-04-22T11:34:41Z

Published version:

DOI:10.1111/jbi.13792

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

Trait-modulated decline of carabid beetle occurrence along elevation gradients across the European Alps

Journal:	<i>Journal of Biogeography</i>
Manuscript ID	Draft
Manuscript Type:	Research Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Chamberlain, Dan; University of Turin, Department of Life Sciences and Systems biology Gobbi, Mauro; MUSE-Science Museum, Section of Invertebrate Zoology and Hydrobiology Negro, Matteo; University of Turin, Department of Life Sciences and Systems biology Caprio, Enrico; University of Turin, Department of Life Sciences and Systems biology Palestrini, Claudia; University of Turin, Department of Life Sciences and Systems biology Pedrotti, Luca; Parco Nazionale dello Stelvio, Lombardia Brandmayr, Pietro; Università della Calabria, Department of Biologia, Ecologia, Scienze della Terra Pizzolotto, Roberto; Università della Calabria, B.E.S.T.; Rolando, Antonio; Università di Torino, Dipartimento di Scienze della Vita e Biologia dei Sistemi
Key Words:	Alpine, carabids, elevation gradient, species traits, body size, wing development

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

**Trait-modulated decline of carabid beetle occurrence along elevation
gradients across the European Alps**

Running title: Trait-elevation interactions in carabids

**Dan Chamberlain^{1*} | Mauro Gobbi² | Matteo Negro¹ | Enrico Caprio¹ | Claudia Palestini¹ | Luca
Pedrotti³ | Pietro Brandmayr⁴ | Roberto Pizzolotto⁴ | Antonio Rolando¹**

*Corresponding author

Email dan.chamberlain99@gmail.com

¹ Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13,
10123, Turin, Italy.

² Section of Invertebrate Zoology and Hydrobiology, MUSE-Science Museum, Corso del Lavoro e della
Scienza, 3 38122, Trento, Italy.

³ Stelvio National Park, Province Autonomous of Trento, via De Simoni 42, 23032, Bormio, Italy

⁴ Department of Biologia, Ecologia, Scienze della Terra, Università della Calabria, Ponte Bucci 4b,
87036 Rende (CS), Italy

ACKNOWLEDGEMENTS

We thank the following people for help in the field: Claudia Tocco, Alice Longoni, Stefano Mammola,
Luca Migliore, Claudio La Rocca, Silvia Ronzani, Andrea Battisti, Laura Leso, Davide Bocola, Cristina
Novara, Sara Calliero, Katia Leo, Cristina Tha, Mauro Paschetta, Nicola Bodino, Gabriele Chiappetta,
Eleonora Operti, Laura Picchi, Luca Corlatti, Duccio Tampucci, Andrea Mustoni, Marco Caccianiga.

Abstract

Aim: To assess how species traits modulate the responses of carabids to elevation gradients, and how consistent these relationships are across different Alpine regions.

Location: Italian Alps.

Taxon: Coleoptera, Carabidae (ground beetles)

Methods: Carabid communities were sampled using pitfall traps along elevation gradients (697-2840 m) in 433 study sites comprising a range of habitat types. The probability of carabid occurrence was modelled in relation to elevation, region and their interactions with two key traits, body size and wing development, using a mixed-modelling framework.

Results: Carabid occurrence declined with increasing elevation, although this relationship was modulated by both body size and wing development. Smaller species were less likely to occur than larger bodied species at lower elevations, but the probability of occurrence of smaller species did not vary greatly across the gradient, whereas for larger species, there was a steep decline in occurrence from low to high elevation. Occurrence of brachypterous species (reduced wings) was greater at lower elevations, but declined steeply as elevation increased, whereas dimorphic and macropterous species (fully winged) declined along the gradient, but less steeply. However, these patterns also varied regionally, indicating that trait-elevation interactions are not geographically consistent. Habitat could not explain the differences between regions.

Main conclusions: Species traits are important in explaining the distribution of carabids along elevation gradients in mountains, and they may help to identify the species that are the most vulnerable, and the most resilient, to future environmental change. Increased probability of occurrence of smaller, winged species at higher elevations suggests that these species are likely to be particularly threatened in the future. However, the difference in responses to elevation between regions has important implications for modelling species distributions, as it suggests low model transferability, i.e. a trait-based model derived from one region cannot necessarily be used to project relative elevational shifts in a wider area.

KEYWORDS

Alpine, carabids, elevation gradient, species traits, body size, wing development.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1 | INTRODUCTION

The study of species traits can provide key insights into mechanisms that drive species distributions, as these traits can modulate species responses to the environment (Pollock et al., 2012). Species' sensitivity to environmental change is in part related to intrinsic factors, so particular traits shown by different species may to some extent dictate their responses (Moretti et al., 2017; Nolte et al., 2019), and ultimately the consequences for the population as a whole. Indeed, there are studies that have demonstrated that particular traits are associated with population declines and local extinction risk (e.g. Kotze & O'Hara 2003; Driscoll & Weir 2005; Nolte et al., 2019). As such, traits can be useful indicators of responses to environmental disturbance (Vanderwalle et al., 2010; Kotze et al., 2011).

Carabid beetles (Coleoptera: Carabidae), also known as ground beetles, are good candidate ecological indicators as they are sensitive to habitat heterogeneity and land-use, they are sufficiently abundant and relatively easy to study (Vanbergen et al., 2005; Gobbi & Fontaneto 2008; Vanderwalle et al., 2010; Gobbi et al., 2015). In carabids, two species traits have been studied in particular, body size and wing development. Body size is well known to vary in relation to environmental gradients in a range of organisms (Blackburn et al., 1999), including carabids (Gutiérrez & Mendez, 1997; Homburg et al., 2013) as it is related to food availability in the environment and to the length of larval development (Blake et al., 1994; Lövei & Magura, 2006). Wing development varies in carabids from species with fully developed hind wings (macropterous) to flightless species with undeveloped hindwings (brachypterous). There are also some species ('dimorphic') which have both macropterous and brachypterous individuals. Wing development is thus a trait which is linked to dispersal ability and hence may be important in terms of how species may respond (i.e. move) to a particular environmental change (Brandmayr 1983; Kotze et al., 2011).

Studying variations in species traits across elevation gradients provides a useful means to assess potential environmental change impacts in mountains in the absence of long-term monitoring data, as this approach provides a space-for-time substitution when considering conditions along the gradient (Hodkinson, 2005). A greater proportion of brachypterous species tend to be found in carabid communities at increasingly higher elevations at both large (Homburg et al., 2013) and small (Maveety & Browne, 2014) scales. However, the relationship between body size and elevation is less clear. In some cases, body size increases with elevation (Cvetkovska-Gjiogjievska et al., 2017), while others have found weak (Pizzolotto et al., 2016), variable (Maveety & Browne, 2014) or no (Homburg et al., 2013) association. However, body size has been shown to be associated with habitat type (Gobbi & Fontaneto, 2008; Pizzolotto et al., 2016), and environmental productivity and stability (Homburg et al., 2013; Nolte et al., 2019). It therefore seems that a number of factors may

affect trait responses to the environment, and it thus follows that such relationships may vary regionally. If species-environment relationships are to be used to draw inferences on species' vulnerability to environmental change, then it is important to understand the extent to which such relationships are consistent over different spatial contexts (e.g. Whittingham et al., 2007), which includes the role of species traits in driving species distributions along ecological gradients.

In this study, we consider the role that two key traits, body size and dispersal ability (represented by hind wing development), play in determining the elevational distribution of carabids in three different regions of the European Alps. Mountains in general, and the European Alps in particular, face a number of pressures including climate change, increasing human disturbance and changes in livestock management, all of which may have potentially profound effects on high elevation biodiversity (e.g. Dirnböck et al., 2011; Payne et al., 2017), and they also harbour a number of endemic and endangered species (e.g. Negro et al., 2008; Rabitsh et al., 2016). As a result of both climate and land use changes, carabid beetles have tended to shift towards summits over the past decades (Pizzolotto et al., 2014), and changes in vegetation have resulted in a reduced area of open habitats, with subsequent negative effects for high elevation species (Pizzolotto et al., 2016). Therefore, an understanding of how traits modulate species responses to elevation gradients may help to identify which species (i.e. with particular traits) may be negatively impacted by, and which species will be resilient to, future environmental change, if we consider our environmental gradient as a climate gradient and a space-for time substitution (Blois et al., 2013). Specifically, we assess how species traits modulate the responses of carabids to elevation and habitat gradients, and importantly, how consistent these relationships are across three main Alpine regions (Western, Central-Eastern and Eastern Alps).

2 | MATERIALS AND METHODS

A database of carabid species presence from a range of different sampling locations in the Italian Alps was compiled from several different studies (a list of sampling locations, years of sampling, and the number of traps set per location is given in Appendix S1). There was a total of 433 sampling sites. There were three main regions of study, corresponding to the three main groups participating in the study (Fig. 1): the Western Alps ($n = 264$ sites, henceforth W-Alps) in Piedmont and Val d'Aosta in the northwest of Italy; the Central-Eastern Alps in the regions of Trentino-Alto Adige (the western part) and Lombardy, ($n = 125$ sites, henceforth CE-Alps); and the Eastern Alps in Trentino-Alto Adige (the eastern part) and the Veneto Dolomites ($n = 44$ sites, henceforth E-Alps).

1
2
3 128 Furthermore, sites were grouped into study areas which referred to the geographic location of a
4
5 129 cluster of sites, often a single valley and from the same study (e.g. a group of sites distributed along
6
7 130 an elevation gradient that were sampled under the same project). All studies adopted the same
8
9 131 general pitfall trapping method: plastic vessels, c. 10 m apart, measuring about 8 cm mouth
10
11 132 diameter, and 10 cm in depth, containing c. 20 ml of an attracting and preserving mixture of white
12
13 133 wine vinegar and sodium chloride, and covered with some rocks (which allowed access to beetles,
14
15 134 but which prevented the trap filling with rain, and discouraged interference from larger animals;
16
17 135 Brandmayr et al., 2005). Modifications for non-lethal traps were made in areas with species of
18
19 136 conservation concern (Negro et al., 2013). The number of traps and the number of days for which
20
21 137 traps were active ('exposure days') varied between sites (respectively a range of 2 to 15 traps per
22
23 138 site, which were active from 14 to 150 days). This variation in effort was taken into consideration in
24
25 139 the analysis (see below).

26
27 140 The database consisted of the presence or absence of each species recorded per site, the
28
29 141 total number of traps used and the total number of exposure days. In addition, broadscale habitat
30
31 142 data from the Corine land cover classification was derived for each site, based on the central grid
32
33 143 coordinate of each site, which comprised the following land cover classes, estimated as percentage
34
35 144 cover within a 100m radius of the central grid coordinate: coniferous forest, mixed forest,
36
37 145 broadleaved forest, grass, shrubs, rock, sparse vegetation, crops, water, snow/glaciers and urban
38
39 146 (henceforth referred to as habitat types). Elevation was also extracted from a Digital Terrain Model.

40
41 147 For each species, mean body length (mm) and hind wing development was obtained from
42
43 148 Brandmayr et al., (2005), Homburg et al., (2014), Gobbi et al., (2015), Gobbi et al., (2017), Pizzolotto
44
45 149 et al., (2016), Hůrka (1996) and direct observations under a stereomicroscope. Body size was centred
46
47 150 and scaled prior to statistical analyses. Wing development was defined into three groups: (i)
48
49 151 brachypterus – flightless species with reduced (wing shorter than the elytron) or absent hind wings,
50
51 152 expected to be poor dispersers; (ii) macropterous – flying species with fully developed hind wings
52
53 153 (unfolded wing longer than the elytron); (iii) dimorphic – species which can show both
54
55 154 brachypterous and macropterous individuals.

56
57 155
58
59 156 **1.1 | Statistical analyses**

60
61 157 The goal of the analyses was to determine the extent to which two specific traits, body size and hind
62
63 158 wing development, modulated the probability of carabid presence along the elevation gradient, the
64
65 159 extent to which the traits effect varied regionally, and the role of habitat in driving both trait-
66
67 160 elevation and trait-region interactions by adopting a mixed modelling approach (following Carboni et
68
69 161 al., 2018).

First, the extent to which body size and the frequency of different wing development types was compared between regions using, respectively, ANOVA and χ^2 -tests. The two traits were then modelled separately using Generalized Linear Mixed Models (GLMMs). The presence of a carabid species at a given site was modelled in relation to elevation, two-way interactions between elevation and region, and elevation and trait, and the interaction between all three variables. Following Carboni et al. (2018), the trait was not modelled as a main effect, but only as an interactive effect, as we were interested in the modulating effect it had on the relationship between elevation and carabid presence. We ran GLMMs using the `glmer` function of the `lme4` package in R. Species identity was included as a random effect as per Carboni et al. (2018). In addition, study area was specified as a further random effect to account for non-independence of sampling sites from the same location and study (Dormann et al., 2007; Gobbi & Brambilla, 2016). Other variables (body size or wing development, elevation, region and land cover variables) were specified as fixed effects. A binomial error distribution was specified. Model outputs estimate the probability of occurrence of the 'average' species across the whole community in relation to fixed effects. Potential residual spatial autocorrelation was examined by plotting variograms (Zuur et al., 2009). Significance of fixed effects was approximated by using the `Anova` function in the `car` package (Fox & Weisberg, 2011). Including all 195 species resulted in convergence problems for many models, hence rare species ($n = 28$) that occurred only once in the whole sample were omitted. The final database consisted of 167 species from 433 sites, making a total of 72311 observations.

Using the above model structure, a series of exploratory analyses were first undertaken to assess effects of sampling effort, and to consider potential biases or model fitting problems by including certain habitats. Effort in terms of both the number of traps and the exposure days varied between sampling locations. In order to assess the potential effect of effort on probability of carabid presence, an initial analysis was carried out using the total number of exposure days \times the number of traps per sampling site as a measure of effort. This variable was log-transformed, centred and standardized before analysis. A GLMM was then run, modelling species presence in relation to linear and quadratic effects of effort, specifying species as a random factor (as above). There was a highly significant effect of both linear ($\chi^2 = 36.22$, $p > 0.0001$) and quadratic effort terms ($\chi^2 = 9.94$, $p > 0.001$), showing the probability of occurrence increased at an accelerating rate with an increase in effort (Appendix S2). Linear and quadratic effort terms were included in all subsequent models to account for this effect.

To address the main objectives, data were first analysed across the whole data set, considering the interaction between trait and elevation. Second, the extent to which the trait-elevation interaction was modulated by region was also considered by adding region, and the three-

way interaction between region, trait and elevation was tested. Where there were significant region interactions, analyses were run separately according to the three regions. Third, the effect of habitat variation was considered by substituting elevation with habitat in the above models. A large number of habitat variables were recorded, and there was a strong degree of inter-correlation between them due to the marked changes in habitat along the elevation gradient considered (e.g. from forest to shrub-forest mosaics to alpine pasture as elevation increases). The habitat data were therefore analysed using Principal Components Analysis (PCA) in order to try and identify meaningful environmental gradients which were then used in subsequent models.

Model performance was assessed by comparing Akaike's Information Criterion (AIC) for models with different fixed effects. Models with lower AIC values are considered to be better performing, and when a difference in AIC between models (ΔAIC) is less than 2, models are considered of equivalent performance (Burnham & Anderson, 2002).

3 | RESULTS

Of the total 195 species recorded, 44% (85 species) were brachypterous, 15% dimorphic (29 species) and 41% macropterous (81 species). Most species were medium sized (5.4-10.75mm, 42%, 81 species), while extra large species were the least frequent (22-35mm, 8%, 16 species). Large species (11-21.5mm, 32%, 62 species) were more frequent than small species (2.7-5.25mm, 18%, 36 species). A total of 19% of species were classed as steno-endemic or endemic, i.e. with very restricted geographical range, e.g. *Carabus olympiae*, *Duvalius breiti*, *Trechus dolomitanus*, while most species (44%) showed wide or very wide distributions, e.g. *Amara eurynota*, *Calathus fuscipes*, *Pseudophonus rufipes*.

3.1 | Habitat description

For most of the 11 habitat types considered, there were either cover values close to 100% or close to 0%, reflecting the fact that most sample sites were either in forest or alpine grasslands and other open habitats above the treeline, with few sites in ecotone habitats. There were also some habitats which were rare, occurring on $\leq 5\%$ of sites across the sample (crops, water, snow/glaciers, and urban). These were not considered further. For the seven other habitats (coniferous forest, mixed forest, broadleaved forest, grass, shrubs, rock, sparse vegetation), cover was converted to presence/absence per site. Differences between regions were then analysed for each of these latter habitat types using a GLM specifying binomial errors. There were a number of significant differences between regions (Table 1). Notably, sampling sites in the W-Alps were more likely to have broad-

leaved and mixed forest and less likely to have sparse vegetation, those in the E-Alps were more likely to have grass, and those in CE-Alps were more likely to have rock. The mean elevation differed between regions ($\chi^2 = 18.13$, $P > 0.001$), where sampling sites in CE-Alps and E-Alps were on average higher than in the W-Alps (mean \pm sd, W-Alps = 1766 ± 33 m, $n = 264$; C-Alps = 1990 ± 48 m, $n = 125$; E-Alps = 1965 ± 57 m, $n = 44$), although E-Alps had a notably smaller elevation range than W-Alps or CE-Alps (respectively 1540m, 2075m and 2126m).

The seven more widespread habitat variables were analysed using PCA. The first two PCA axes accounted for 37% of variation in the data. The first axis represented a gradient from closed (coniferous forest) to open (grassland and rock) habitats, whereas the second axis was a gradient from broadleaved and mixed forest to coniferous forest and grassland, and was therefore representative of the elevation gradient (Appendix S2). Indeed, Axis 2 was positively correlated with elevation ($r = 0.45$), whereas Axis 1 was less strongly and negatively correlated with elevation ($r = -0.32$). Lower axes were harder to interpret and were not considered further.

3.2 | Trait and elevation

Overall, the probability of carabid occurrence decreased with increasing elevation. This is reflective of the general decrease in species richness with elevation (Poisson regression with study area as a random effect, slope \pm se = -0.558 ± 0.059 , $p < 0.0001$). There was a significant negative effect of elevation on the probability of carabid occurrence which was modulated by body size (Fig. 2), as shown by the significant interaction between elevation and body size ($\chi^2 = 102.70$, $p > 0.0001$; note full model details are given in Appendix S3). This means that the probability of occurrence increased with smaller body sizes at higher elevations, whereas species with larger body sizes were much more likely to occur at lower elevations, and this probability declined rapidly at higher elevations. There was also a significant interactive effect of elevation and wing development on the probability of carabid occurrence ($\chi^2 = 44.21$, $p < 0.001$). In this case, the probability of occurrence of brachypterous species (low dispersal) was highest at lower elevations, but decreased markedly as elevation increased, whereas for the other two categories, the rate of decrease was much less (Fig. 3). The body size model was a better fit than the wing development model ($\Delta AIC = 63.6$), suggesting body size has a greater modulating effect than wing development. There was a suggestion of residual spatial autocorrelation in that there was some trend evident in the residuals (Appendix S4).

Note that estimates of probability of occurrence in the figures are for an average species. Given that the overall occurrence rate (i.e. the number of presences as a proportion of the total number of site \times species combinations) was 0.042, these probabilities are small. Nevertheless, the patterns were generally consistent when considering only more widespread species. For example,

the models testing for interactions between trait and elevation were generally similar, especially body size, to those above when considering only the 49 species which occurred in at least 20 sites (Appendix S5).

3.3 | Region effects

The next stage was then to assess whether the above models were influenced by region (full model details are given in Appendix S3). There was no evidence of an overall difference in body size between regions (ANOVA comparing body sizes of all species present in each region: $F_{2,182} = 0.31$, $p = 0.73$). In the mixed effects model, there was a significant three-way interaction between body size, elevation and region ($\chi^2 = 34.79$, $p > 0.0001$). This model was better performing than the elevation-only model in terms of AIC ($\Delta\text{AIC} = 38.0$), suggesting important additional variation is explained by region. Therefore, the interactions were considered separately by region. Patterns in W-Alps and E-Alps were similar to each other, and to the overall model (Fig. 4), although probability levels were somewhat lower in the latter region. The interaction between body size and elevation was significant in both regions (W-Alps $\chi^2 = 144.11$, $p > 0.0001$; E-Alps $\chi^2 = 13.85$, $p > 0.001$). CE-Alps, however, showed a rather different pattern (Fig. 4B) and there was no significant interaction between body size and elevation ($\chi^2 = 0.80$, $p = 0.37$). Instead, there was a rather uniform decrease in probability of occurrence with increasing elevation across different body sizes – in other words the probability of occurrence of carabids of small or large body size was equal for any given elevation. For all three regions, there was less evidence of spatial autocorrelation in the data according to variograms (Appendix S4) compared to the model without region (i.e. Fig. 2).

There was no evidence that the frequency of the different wing development classes was associated with any particular region ($\chi^2_4 = 7.41$, $p = 0.13$). In common with body size, there was a significant three-way interaction between wing development, elevation and region ($\chi^2 = 195.45$, $p > 0.0001$) in the model, which was much better performing than the elevation-only model ($\Delta\text{AIC} = 329.6$). When analysed separately by region, there was a highly significant interaction between wing development and elevation in W-Alps ($\chi^2 = 173.21$, $p > 0.0001$) and CE-Alps ($\chi^2 = 19.88$, $p > 0.0001$), but not in E-Alps ($\chi^2 = 4.13$, $p = 0.13$). The probability of occurrence of brachypterous species decreased with elevation in W-Alps, whereas there was an increase in macropterous and dimorphic species (Fig. 5A). However, in CE-Alps, there were declines in the probability of occurrence of all three groups with elevation (Fig. 5B).

The W-Alps region covered a larger geographic range than the other two regions, including three study areas from the Maritime Alps in the south-western area of the Alpine arc (Fig. 1). Including the Maritime Alps as a separate region resulted in model convergence problems. Omitting

these three study areas ($n = 17$ sites), however, had no marked effect on the outcomes of either the elevation model, nor the regional model, for either trait (Appendix S6).

3.4 | Habitat effects

Elevation was substituted by, separately, Axis 1 and Axis 2 (i.e. two separate models) in the body size- elevation model for all regions (i.e. that in Fig. 1) in order to assess if habitat variations could explain the effect of elevation (model details are given in Appendix 7). There was no significant interaction between body size and Axis 1 ($\chi^2 = 0.031$, $p = 0.86$) or Axis 2 ($\chi^2 = 0.257$, $p = 0.61$). Similarly, there was no evidence that the body size-elevation association varied according to region (i.e. no significant PCA axis \times elevation \times region interaction) for either Axis 1 ($\chi^2 = 0.857$, $p = 0.65$) or Axis 2 ($\chi^2 = 0.200$, $p = 0.91$). In common with body size, there was no evidence of an interactive effect between habitat and wing development on the probability of carabid occurrence (Axis1*wing development, $\chi^2 = 1.08$, $p = 0.58$; Axis2*wing development, $\chi^2 = 1.40$, $p = 0.50$), nor was there evidence of a three-way interaction with region (Axis1 $\chi^2 = 10.77$, $p = 0.10$; Axis2 $\chi^2 = 2.68$, $p = 0.85$). Model performance was always worse in habitat models ($\Delta AIC > 90$).

4 | DISCUSSION

There was a general decline in probability of carabid occurrence along the elevation gradient in all models, reflecting the decrease in species richness at higher elevations. This result is in agreement with carabid species richness patterns investigated in other mountain areas (e.g. Maveety et al., 2011; Zou et al., 2014; Winkler et al., 2018). Our results highlighted that the studied species traits (i.e. body size and wing morphology) take part in modulating the species richness elevational trend, but that these relationships were in general not consistent across different Alpine regions.

In general, smaller species were less likely to occur than larger bodied species at lower elevations, but the probability of occurrence of smaller species did not vary greatly across the gradient, whereas for larger species, there was a steep decline in occurrence from low to high elevation. Body size is correlated with many aspects of carabid life history, i.e. reproductive rate, dispersal, resource utilization, energetic balance and competition (Homburg et al., 2013; Nolte et al., 2019). A change in body size of a population in a habitat may indicate environmental stress (Blake et al., 1994; Garbalińska & Skłodowski, 2008). Smaller species can be found at all elevations: we found that they are relatively more likely to live at high elevations compared to larger species, where they show a shorter larval development that likely enables them to exploit the short snow-free season

when reproduction is possible. This seems to follow the hypothesis of the negative effect of elevation on body size (Horne et al., 2017). In addition, most of the small species living at medium-low altitudes in riparian habitats or human-managed areas have completely developed wings, thus they are able to disperse better, and so they respond quickly to environmental stress/perturbation, hence they are dominant in harsher, less predictable conditions (Brandmayr, 1983, 1991; Pizzolotto, 2009). The occurrence of larger species is positively linked to the successional stage of a habitat, whereas it is negatively linked to environmental stress (Melis et al., 2010; Gobbi & Fontaneto, 2008). At low elevations, larger carabids are dominant in woodlands, their occurrence declining with increasing elevation due to climatic and trophic, and thus ultimately physiological, constraints that positively select for small size species.

There was an analogous pattern in relation to wing development, where brachypterous species occurrence was greater at lower elevations, but declined steeply as elevation increased, whereas dimorphic and macropterous species declined along the gradient, but less steeply. It was notable that dimorphic and macropterous species showed very similar trends in all models, suggesting that species with variable wing development are similar ecologically to fully macropterous species (as per Homburg et al., 2013). A greater prevalence of brachypterous species along the elevation gradient has been reported for insects in general (Hodkinson, 2005), and carabids in particular (Homburg et al., 2013; Maveety & Browne 2014), and has been explained by reduced flight activity in harsh cold environments (Hodkinson, 2005) where wind is also likely a limiting factor. Our results do not support this contention, showing instead a marked decrease in brachypterous compared to macropterous or dimorphic species along the elevation gradient. Rather, our results support the hypothesis of Brandmayr (1991) who tried to draw the evolutionary pathway leading to wing reduction in carabid beetles. He assumed that the amount of brachypterous species increases among two main axes interacting in an additive way: the dynamic stability of a habitat (successional stages) and the hydric stability of the soil (water balance). Brachypterous species likely have a lower gene flow with respect to macropterous species because they have low dispersal abilities. Therefore, they are prone to local extinction due to strong environmental perturbations, thus unlike macropterous species that are potentially able to shift on all kind of habitats, brachypterous species are linked to low elevation natural and climax habitats (i.e. stable successional stages such as mountain forests). The progressive and marked decline of brachypterous species as elevation increases can thus be explained by increasing environmental and micro-climatic pressure at high elevation: only few brachypterous species are adapted to live above c. 2000 m, because these elevations are characterized by lower food availability, low annual mean temperatures, and shorter breeding and growing seasons. Species able to fly are likely more able to

maintain more connected subpopulations of a metapopulation in the patchy habitats located above the treeline.

Relationships between traits and elevation showed some notable regional variations, suggesting that the way traits modulate the occurrence-elevation relationship are not consistent geographically. Pizzolotto et al. (2016) found that in some mountain groups, species traits were weakly correlated with elevation, but were instead more directly driven by the habitat type. We might therefore expect that regional differences could be explained on the basis of habitat variations. However, there was no evidence that habitat was associated with carabid occurrence, nor that this was modulated by traits, both overall and at regional levels. Elevation provided a better model fit in each case, suggesting that elevation relationships are not driven by habitat variations. It should be noted, however, that the habitat data used were based on land cover types that were more related to general habitat structure than vegetation species composition, hence we can only draw conclusions about habitat measured at a fairly coarse resolution. It is possible that finer-scale micro-habitats, in particular plant species, topography or microclimate, and the degree of human disturbance, can all play important roles.

Climate is likely to be a key driver in the overall relationship between occurrence, elevation and traits, as smaller and better dispersing (i.e. macropterous) species are better adapted to harsher conditions at high elevation (Brandmayr, 1991; Okuzaki et al., 2015). We have used elevation as a proxy for climatic conditions, as the elevation gradient is correlated with a range of environmental factors, most notably temperature, but also precipitation, atmospheric pressure, wind speed, and radiation input (Barry, 1992), all of which may influence carabid distributions along elevation gradients through physiological constraints triggered by the climatic conditions (Hodkinson, 2005). Variations between regions may therefore be due to a range of climatic influences in addition to temperature, and their effects may interact with each other and with other factors such as topography. Teasing apart the precise elements that dictate regional differences in carabid distributions therefore represents a challenge.

Climate change is likely to threaten high elevation species in particular as they are pushed increasingly towards mountain summits, and eventually these species may have 'nowhere to go' as these summits become climatically unsuitable (e.g. Dirnböck et al., 2011; Pizzolotto et al., 2016). This study suggests that smaller, winged carabids are likely to be most vulnerable to such climate change impacts, and also that species with these characteristics would be good candidate indicators of environmental change in mountains (Brandmayr et al., 2013). However, it is also important to highlight that among the steno-endemic species, which are all low dispersal species and cover a wide body size range, from medium-large species (e.g. *Carabus* spp., *Oreonebria* spp.) to smaller-sized

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

species (*Trechus* spp.), local extinctions have been already documented (Pizzolotto et al., 2014), thus they must also be considered very sensitive to environmental and climate change in mountains.

The difference in responses to elevation between regions has important implications for modelling species distributions, as it suggests low model transferability, i.e. a trait-based model derived from one region cannot necessarily be used to project relative elevational shifts in a wider area. In order to improve our understanding of regional differences in how traits modulate carabid distributions along elevation gradients, the contributions of individual climatic components, as well as the effects of finer-scale habitat features, need to be assessed.

ORCID

- Dan Chamberlain <https://orcid.org/0000-0002-5381-2024>
- Mauro Gobbi <https://orcid.org/0000-0002-1704-4857>
- Roberto Pizzolotto <https://orcid.org/0000-0002-4587-3476>
- Pietro Brandmayr <https://orcid.org/0000-0002-6753-4897>

TABLE 1. Parameter estimates \pm se for the probability of occurrence (on a logit scale) of habitats across carabid sampling sites in the Italian Alps. % freq, indicates the percentage of presences across the sample of 433 sites. W-Alps n = 264, CE-Alps n = 125, E-Alps n = 44.

Habitat	% freq.	W-Alps	CE-Alps	E-Alps	χ^2	<i>p</i>
Coniferous forest	34	-0.693 ± 0.131	-0.419 ± 0.182	-1.068 ± 0.349	3.21	0.20
Broad-leaved forest	16	-1.119 ± 0.143	-4.127 ± 0.713	-3.738 ± 1.011	51.80	<0.001
Mixed forest	12	-1.530 ± 0.161	-2.99 ± 0.418	-3.738 ± 1.012	20.74	<0.001
Grass	34	-0.626 ± 0.129	-1.036 ± 0.203	0.140 ± 0.306	10.50	0.005
Shrubs	9	-2.741 ± 0.258	-1.858 ± 0.261	-2.277 ± 0.525	5.74	0.057
Rock	16	-1.946 ± 0.186	-1.112 ± 0.207	-1.819 ± 0.440	8.85	0.012
Unvegetated	6	-4.466 ± 0.581	-2.162 ± 0.292	-1.194 ± 0.361	33.52	<0.001

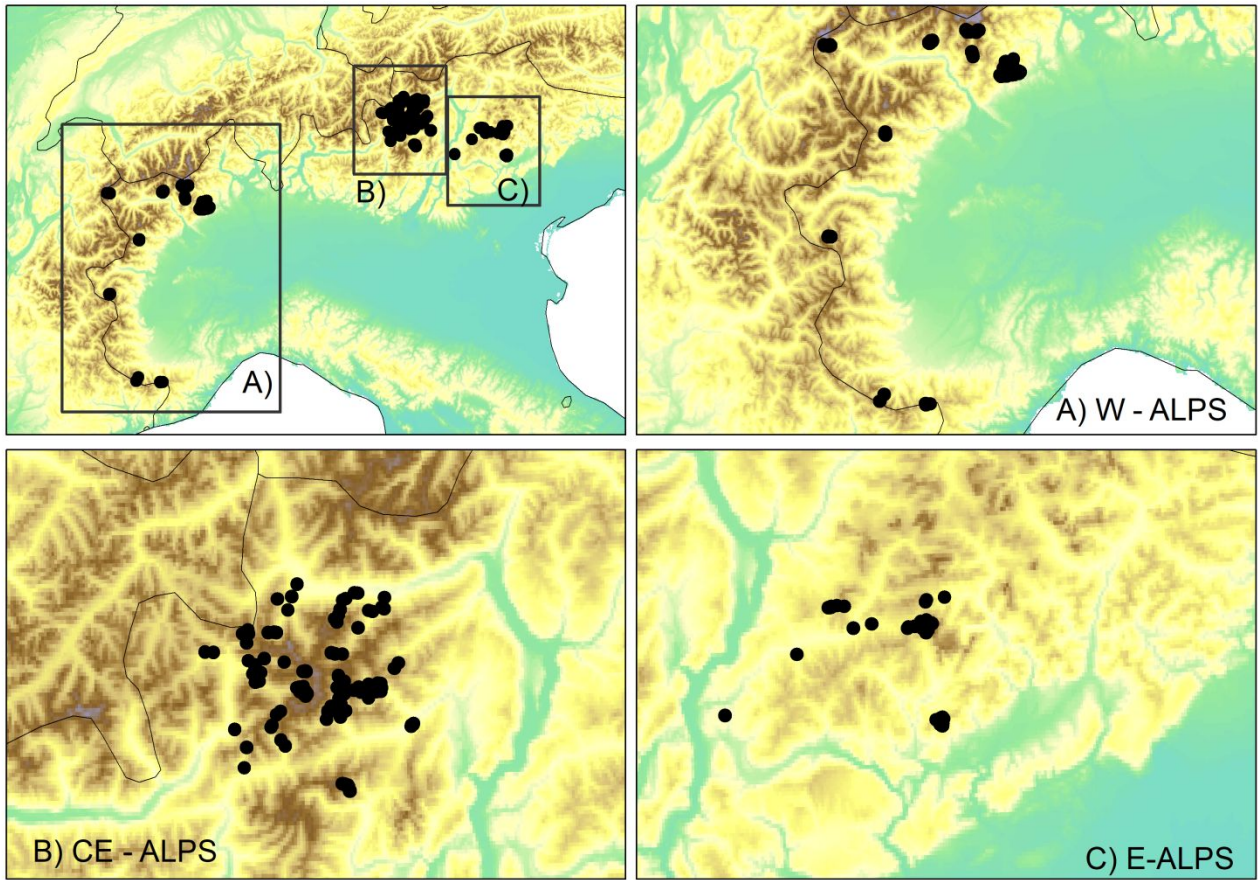


FIGURE 1. Study area in the Italian Alps, showing the 433 study sites (black dots) and the three regions considered.

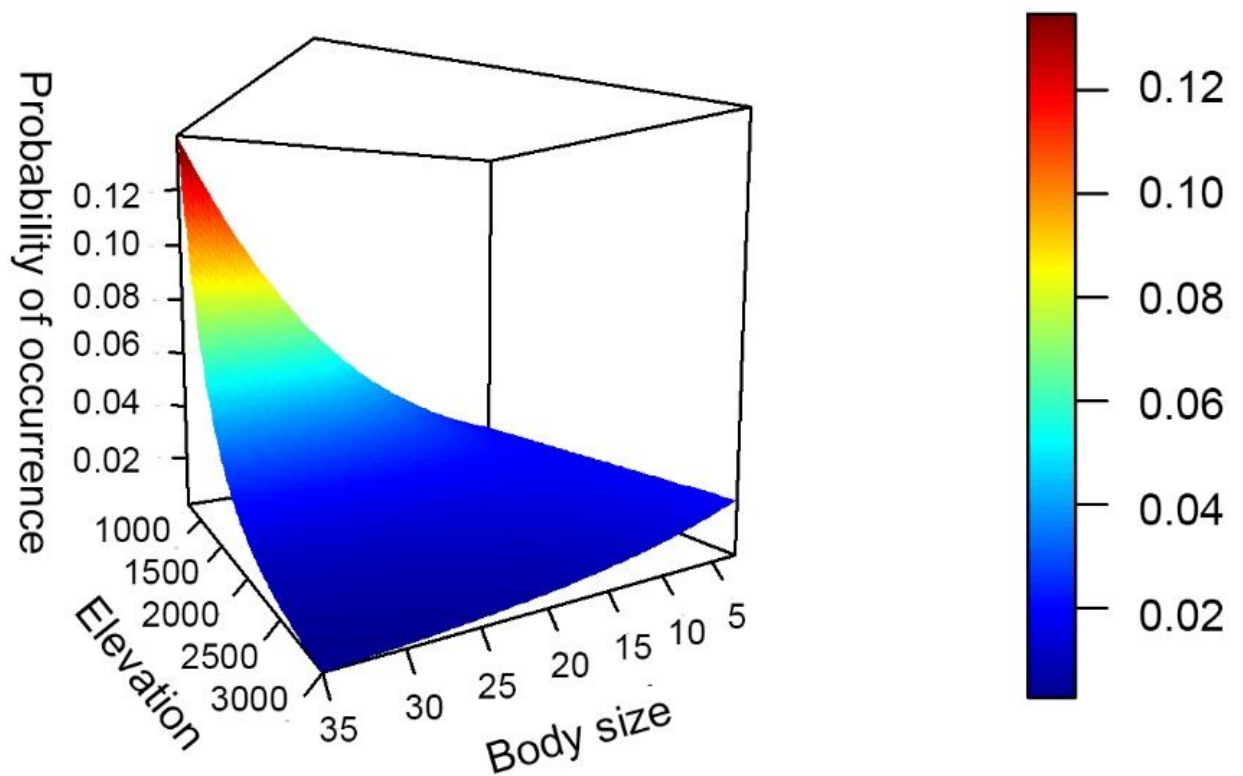


FIGURE 2. Probability of carabid presence in relation to elevation and body size combining data from all regions.

430

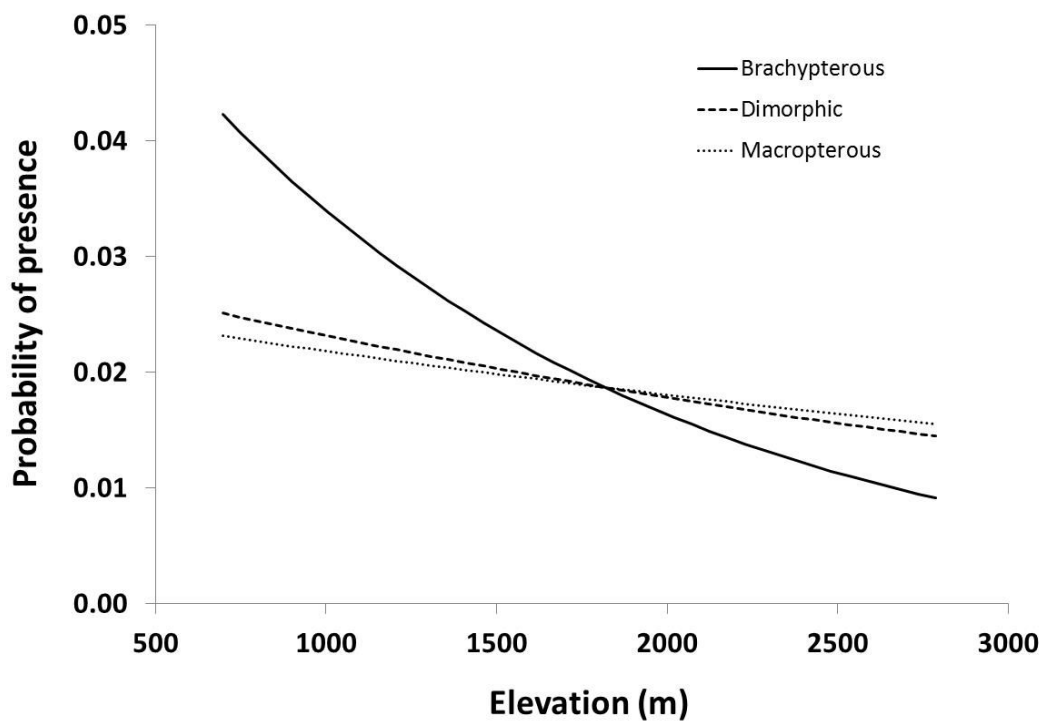
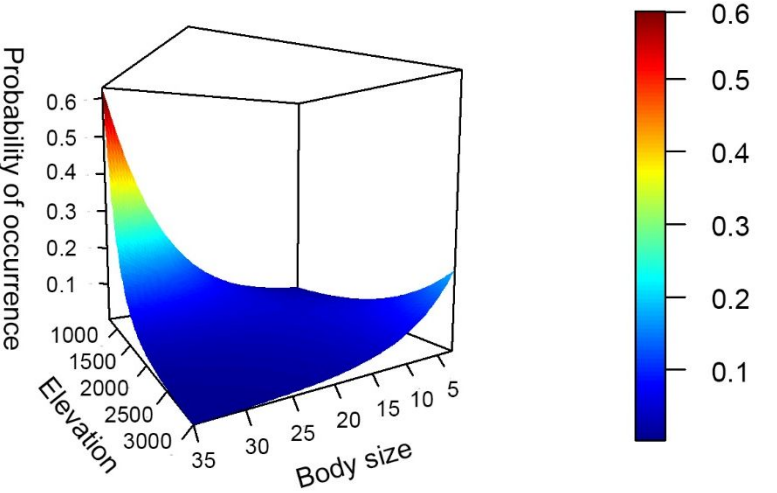
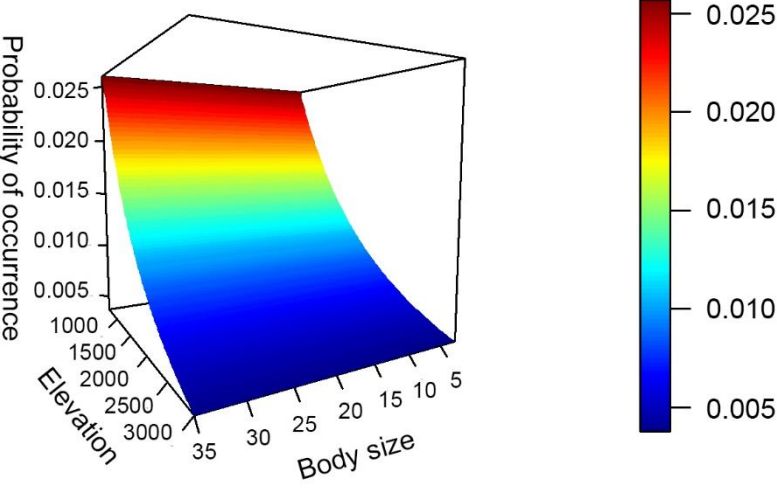


FIGURE 3. Probability of carabid presence in relation to elevation and wing development combining data from all regions.

A. W-Alps



B. CE-Alps



C. E-Alps

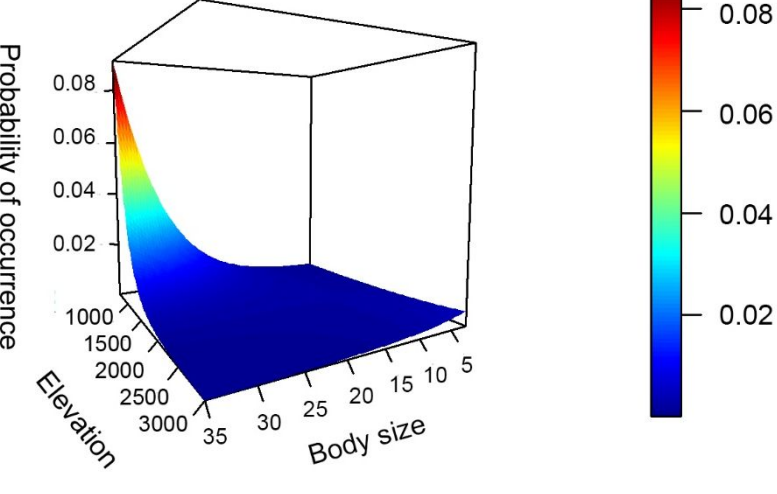


FIGURE 4. Probability of carabid presence in relation to elevation and body size in different Alpine regions.

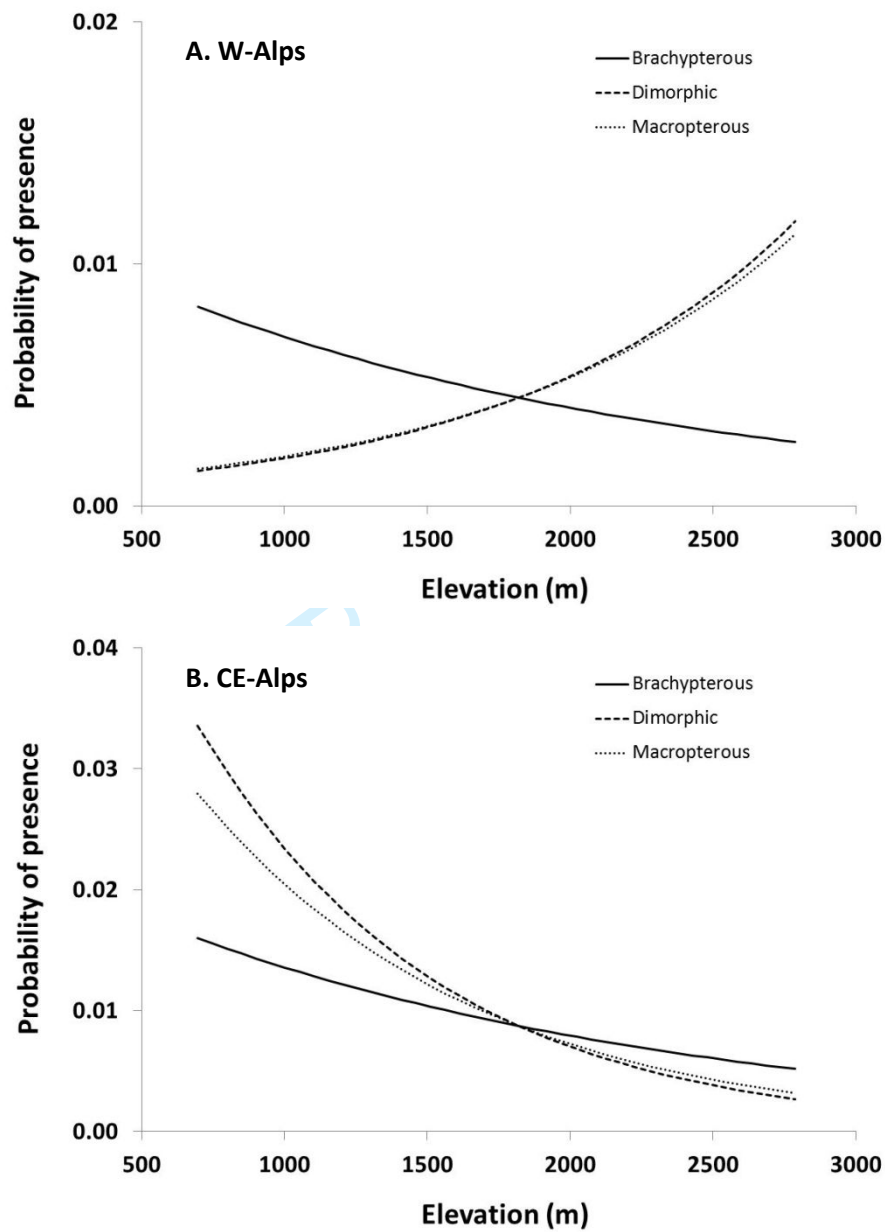


FIGURE 5. Probability of carabid presence in relation to elevation and wing development in different Alpine regions where there was a significant elevation×region×trait interaction. Note that there was no significant region interaction in E-Alps.

REFERENCES

- Barry, R.G. (1992). Mountain climatology and past and potential future climatic changes in mountain regions – a review. *Mountain Research and Development*, 12, 71–86.
- Blackburn, T.M., Gaston, K.J. & Loder, N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity & Distributions*, 5, 165–174.
- Blake, S., Foster, G.N., Eyre, M.D., & Luff, M.L. (1994). Effects of habitat type and grassland management practice on the body size distribution of carabid beetles. *Pedobiologia*, 28, 502–512.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *PNAS*, 110, 9374–9379.
- Brandmayr, P. (1983). The main axes of the coenoclineal continuum from macroptery to brachyptery in carabid communities of the temperate zone. Report 4th Symposium. European Carabidologists, Haus Rothenberge, Westphalia, Sept. 2426/1981, Pubbl. Agric. Univ. Wageningen.
- Brandmayr, P. (1991). The reduction of metathoracic alae and dispersal power of carabid beetles along the evolutionary pathway into the mountains. In: Lanzavecchia G, Valvassori R (eds) *Selected Symposia and Monographs U.Z.I. Mucchi*, Modena, p 363–378.
- Brandmayr, P., Zetto, T., & Pizzolotto, R. (2005). I Coleotteri Carabidi per la valutazione ambientale e la conservazione della biodiversità. Manuale operativo. APAT - Agenzia nazionale per la protezione dell'ambiente e per i servizi tecnici Roma. Manuali e linee guida, 34.
- Brandmayr, P., Giorgi, F., Casale, A., Colombetta, G., Mariotti, L., Vigna Taglianti, A., Weber, F., & Pizzolotto, R. (2013). Hypogean carabid beetles as indicators of global warming? *Environmental Research Letters*, 8, 1–11.
- Burnham, K.P., & Anderson, D.R. (2002). *Model selection and multimodel inference. A practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York, USA.
- Carboni, M., Calderon-Sanou, I., Pollock, L., Violle, C., DivGrass Consortium, & Thuiller, W. (2018). Functional traits modulate the response of alien plants along abiotic and biotic gradients. *Global Ecology & Biogeography* DOI: 10.1111/geb.12775
- Cvetkovska-Gjorgjievska, A., Hristovski, S., Prelić, D., Šerić Jelaska, L., Slavevska-Stamenković, V., & Ristovska, M. (2017). Body size and mean individual biomass variation of ground-beetles community (Coleoptera: Carabidae) as a response to increasing altitude and associated vegetation types in mountainous ecosystem. *Biologia*, 72, 1059–1066.

1
2
3 470 Dirnböck, T., Essl, F., & Babitsch, W. (2011). Disproportional risk for habitat loss of high-altitude
4
5 471 endemic species under climate change. *Global Change Biol.*, 17, 990-996.
6
7 472 Dormann, C., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl G., Davies R.G., Hirzel, A.,
8
9 473 Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B.,
10 474 Schurr, F.M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis
11
12 475 of species distributional data: A review. *Ecography*, 30, 609–628. doi:10.1111/j.2007.0906-
13 476 7590.05171.x.
14
15 477 Driscoll, D.A., & Weir, T. (2005). Beetle responses to habitat fragmentation depend on ecological
16
17 478 traits, habitat condition, and remnant size. *Conservation Biology*, 19, 182-194.
18
19 479 Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression*, Second Edition. Thousand
20 480 Oaks CA: Sage.
21
22 481 Garbalińska, P., & Skłodowski, J. (2008). Body size differentiation in selected carabid species
23
24 482 inhabiting Puszcza Piska forest stands disturbed by the hurricane. *Baltic J. Coleopterol.*, 8, 101-
25 483 114.
26
27 484 Gobbi, M. & Brambilla, M. 2016. Patterns of spatial autocorrelation in the distribution and diversity
28
29 485 of carabid beetles and spiders along Alpine glacier forelands. *Italian Journal of Zoology*, 83: 600-
30 486 605.
31
32 487 Gobbi, M. & Fontaneto, D. (2008). Biodiversity of ground beetles (Coleoptera: Carabidae) in different
33
34 488 habitats of the Italian Po lowland. *Agriculture, Ecosystems and Environment*, 127, 273–276.
35
36 489 Gobbi, M., Fontaneto, D., Bragalanti, L., Pedrotti, L. & Lencioni, V. 2015. Carabid beetle (Coleoptera:
37 490 Carabidae) richness and functional traits in relation to differently managed grasslands in the
38
39 491 Alps. *Annales- Societe Entomologique de France* 51(1).
40
41 492 Gutiérrez, D., & Mendez, R. (1997). Patterns in the distribution, abundance and body size of carabid
42
43 493 beetles (Coleoptera:Caraboidea) in relation to dispersal ability. *Journal of Biogeography*, 24,
44 494 903-914.
45
46 495 Hodkinson, I.D. (2005). Terrestrial insects along elevation gradients: species and community
47
48 496 responses to altitude. *Biol. Rev.*, 80, 489–513.
49
50 497 Homburg, K., Schuldt, A., Drees, C., & Assmann, T. (2013). Broad-scale geographic patterns in body
51
52 498 size and hind wing development of western Palaearctic carabid beetles (Coleoptera: Carabidae).
53 499 *Ecography*, 36, 166–177.
54
55 500 Homburg, K., Homburg, N., Schafer, F., Schuldt, A., & Assmann, T. (2014) Carabids.Org—a dynamic
56
57 501 online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and*
58
59 502 *Diversity*, 7, 195–205.
60

- 503 Horne, C., Hirst, A.G., & Atkinson, D. (2017). Insect temperature-body size trends common to
504 laboratory, latitudinal and seasonal gradients are not found across altitudes. *Functional Ecology*,
505 32, 948-957.
- 506 Hůrka, K. (1996). *Carabidae of the Czech and Slovak Republics*, Česká a Slovenská republiky.
507 Kabourek, Zlin, Czech Republic.
- 508 Kotze, D.J., & O'Hara, R.B. (2003). Species decline – but why? Explanations of carabid beetle
509 (Coleoptera, Carabidae) declines in Europe. *Oecologia*, 135, 138–148.
- 510 Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G. L.,
511 Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J.,
512 Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R., & Zetto, T. (2011) Forty years of
513 carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to
514 bioindication, habitat assessment and conservation. *ZooKeys* 100: 55–148 (2011); doi:
515 10.3897/zookeys.100.1523 - www.zookeys.org
- 516 Lövei, G.L., & Magura, T. (2006). Body size changes in ground beetle assemblages – a reanalysis of
517 Braun et al., (2004)'s data. *Ecol. Entomol.*, 31, 411–414.
- 518 Maveety, S.A. & Browne, R.A. (2014). Patterns of morphology in carabid beetles (Coleoptera:
519 Carabidae) along a Neotropical altitudinal gradient. *International Journal of Tropical Insect*
520 *Science*, 34, 157–171.
- 521 Maveety, S.A., Browne R.A., & Erwin, T.L. (2011). Carabidae diversity along an altitudinal gradient in
522 a Peruvian cloud forest (Coleoptera). *Zookeys*, 147, 651–666.
- 523 Melis, C., Bjerk Olsen, C., Hyllvang, M., Gobbi, M., Stokke, B.G., & Røskoft, E. (2010). The effect of
524 traffic intensity on ground beetle (Coleoptera: Carabidae) assemblages in central Sweden.
525 *Journal of Insect Conservation*, 14, 159–168.
- 526 Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcaràte, F.M., Bell, J.R., Fournier, B.,
527 Hedde, M., Hotral, J., Ibanez, S., Ockinger, E., Sousa, J.P., Ellers, J., & Berg, M.P. (2017).
528 Handbook of protocols for standardized measurement of terrestrial invertebrate functional
529 traits. *Functional Ecology*, 3, 558-567.
- 530 Negro, M., Casale, A., Migliore, L., Palestini, C., & Rolando, A. (2008). Habitat use and movement
531 patterns in the endangered ground beetle species, *Carabus olympiae* (Coleoptera: Carabidae).
532 *Eur. J. Entomol.*, 105, 105–112.
- 533 Negro, M., La Rocca, C., Ronzani, S., Rolando, A., & Palestini, C. (2013). Management tradeoff
534 between endangered species and biodiversity conservation: The case of *Carabus olympiae*
535 (Coleoptera: Carabidae) and carabid diversity in north-western Italian Alps. *Biological*
536 *Conservation*, 157, 255–265.

- 537 Nolte, D., Boutaud, E., Kotze, D.J., Schuldt, A., & Assmann, T. (2019). Habitat specialization,
538 distribution range size and body size drive extinction risk in carabid beetles. *Biodiversity and*
539 *Conservation* DOI: 10.1007/s10531-019-01724-9
- 540 Okuzaki, Y., Sugawara, H., & Sota, T. (2015). Body size evolution under character release in the
541 ground beetle *Carabus japonicus*. *J. Biogeog.*, 42, 2145–2158
- 542 Payne, D., Spehn, E.M., Snethlage, M., & Fischer, M. (2017). Opportunities for research on mountain
543 biodiversity under global change. *Current Opinion in Environmental Sustainability*, 29, 40-47.
- 544 Pizzolotto, R. (2009). Characterization of different habitats on the basis of the species traits and
545 ecofield approach. *Acta Oecologica*, 35, 142–148.
- 546 Pizzolotto, R., Gobbi, M. & Brandmayr, P. (2014). Changes in ground beetle assemblages above and
547 below the treeline of the Dolomites after almost 30 years (1980/2009). *Ecology & Evolution*, 4,
548 1284–1294.
- 549 Pizzolotto, R., Albertini, A., Gobbi, M., & Brandmayr, P. (2016). Habitat diversity analysis along an
550 altitudinal sequence of alpine habitats: the Carabid beetle assemblages as a study model.
551 *Periodicum Biologorum*, 118, 241-254.
- 552 Pollock, L-J., Morris, W.K., & Vesk, P.A. (2012). The role of functional traits in species distributions
553 revealed through a hierarchical model. *Ecography*, 35, 716–725.
- 554 Rabitsch, W., Graf, W., Huemer, P., Kahlen, M., Komposch, C., Paill, W., Reischütz, A., Reischütz, P.L.,
555 Moser, D. & Essl, F. (2016). Biogeography and ecology of endemic invertebrate species in
556 Austria: A cross-taxon analysis. *Basic & Applied Ecology*, 17, 95-105.
- 557 Vanbergen, A.J., Woodcock, B.A., Watt, A.D., & Niemelä, J. (2005). Effect of land-use heterogeneity
558 on carabid communities at the landscape scale. *Ecography*, 28, 3-16.
- 559 Vanderwalle, M., de Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R.,
560 Harrison, P.A., Lavorel, S., Martins da Silva, P., Moretti, M., Niemelä, J., Santos, P., Sattler, T., &
561 Sousa, J.P. (2010). Functional traits as indicators of biodiversity response to land use changes
562 across ecosystems and organisms. *Biodivers. Conserv.*, 19, 2921–2947.
- 563 Whittingham, M.J., Krebs, J.R., Swetnan, R.D., Vickery, J.A., Wilson, J.D., & Freckleton, R.P. (2007).
564 Should conservation strategies consider spatial generality? Farmland birds show regional not
565 national patterns of habitat association. *Ecol. Lett.*, 10, 25-35.
- 566 Winkler, M., Illmer, P., Querner, P., Fischer, B.M., Hofmann, K., Lamprecht, A., Praeg, N., Schied, J.,
567 Steinbauer, K., & Pauli, H. (2018). Side by side? Vascular plant, invertebrate, and microorganism
568 distribution patterns along an alpine to nival elevation gradient. *Arctic, Antarctic, and Alpine*
569 *Research*, 50:1, e1475951.

- 570 Zou, Y., Sang, W., Zhou, H., Huang, L. & Axmacher, J.C. (2014). Altitudinal diversity patterns of
571 ground beetles (Coleoptera: Carabidae) in the forests of Changbai Mountain, Northeast China.
572 *Insect Conservation and Diversity*, 7, 161–171.
- 573 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M., 2009. *Mixed Effects Models and*
574 *Extensions in Ecology with R*. Springer, New York

For Peer Review

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Biosketch

Dan Chamberlain works on impacts of environmental change on animal biodiversity, and has a special interest in the ecology of high elevation species, and how they are likely to be affected by climate change. He is an Associate Professor in Animal Ecology at the University of Turin.

Author contributions: AR conceived the concept of the paper; DC analysed the data; all other authors collected the data and helped compile the database; DC and MB led the writing with contributions from all authors.

For Peer Review

Appendix 1. Site details.

Table S1. Locations of study areas, years sampling undertaken and references if relevant. Coordinates (EPSG 32632) are given for the approximate central sampling site.

Region	Study area	Geographic coordinates (easting; northing)	No. sites	No. traps/site	Year	Reference
CE-Alps	Val D'Amola	632064; 5117932	15	3	2011-12	Gobbi et al. 2017
W-Alps	Argentera	335649; 4975695	5	3-8	2010	Unpubl.
W-Alps	Bettaforca	405849; 5079719	24	4	2010	Negro et al. 2013a
W-Alps	Monte Bianco Miage	336054; 072292	6	6	2006	Gobbi et al. 2011
CE-Alps	Braulio	608061; 5152841	4	5	2013-14	Unpubl.
E-Alps	Passo Rolle, Pale di S. Martino	693850; 5135550	29	3-6	2008-9	Brandmayr & Zetto Brandmayr 1988; Pizzolotto et al. 2014; Unpubl.
CE-Alps	Val Cedec Pasquale	621721; 5145647	5	6	2007	Gobbi et al. 2010
E-Alps	Vette di Feltre	719800; 5108200	14	3-6	1983-4	Brandmayr & Pizzolotto 1987
CE-Alps	Valle dei Forni	620990; 5141563	13	6	2004-05	Gobbi et al. 2007
W-Alps	Gabiet	411470; 5079782	24	4	2007	Negro et al. 2010; 2013a
CE-Alps	Val Grande	607084; 5124529	6	5	2013-14	Unpubl.
W-Alps	Gressoney	409104; 5066965	25	3	2006	Negro et al. 2009
W-Alps	Gressoney La Trinità	406669; 5079314	4	2-7	2010	Unpubl.
C-Alps	Laas	630223; 5162607	8	5	2014-15	Unpubl.
W-Alps	Val Grande, Lanzo	364285; 5027361	3	5-8	2010	Unpubl.
W-Alps	Limone Piemonte	385060; 4890223	8	12	2011	Unpubl.
W-Alps	Lourusa	363909; 4895302	4	12	2008	Unpubl.
CE-Alps	Val Martello	635104; 5155380	9	5	2014-15	Unpubl.
C-Alps	Val di Peio	628040; 5135496	21	3-15	2008-14	Gobbi et al. 2013; 2015; Unpubl.
E-Alps	Altopiano di Pine	669654; 5110691	1	15	2009	Unpubl.
C-Alps	Val di Rabbi	641274; 5140947	17	5-15	2008-14	Gobbi et al. 2013; 2015; Unpubl.
W-Alps	Monte Rosa	417142; 5091161	3	6	2014	Tampucci et al. 2017
CE-Alps	Sobretta Gavia	612125; 5140636	6	5	2013-14	Unpubl.
CE-Alps	Val di Sole	646227; 5133203	4	3	2013-14	Gobbi et al. 2013; 2015; Unpubl.
CE-Alps	Stilfs	610871; 5155656	7	5	2014-15	Unpubl.
W-Alps	Torgnon	388579; 5075027	48	3	2006	Negro et al. 2009
CE-Alps	Val d'Ultimo	645380; 5151327	2	5	2014-15	Unpubl.
CE-Alps	Val di Dentro	598626; 5150057	3	5	2013-14	Unpubl.
W-Alps	Valletta	361744; 4891722	5	12	2008	Unpubl.
W-Alps	Val Sessera	612207; 5148526	105	5	2010	Negro et al. 2013b
CE-Alps	Val Zebrù	612197; 5148496	5	5	2013-14	Unpubl.

References

- Bragalanti, N., Lencioni, V., & Pedrotti, L. (2013) Contributo alla conoscenza delle comunità di carabidi (Coleoptera: Carabidae) del Parco Nazionale dello Stelvio (Settore Trentino). *Bollettino del Museo Civico di Storia Naturale di Verona*, 37:123-130.
- Brandmayr, P. & Pizzolotto, R. (1987) Aspetti zoocenotici e biogeografici dei popolamenti a Coleotteri Carabidi nella fascia alpina delle Vette di Feltre (Belluno). *Biogeographia*, 13: 713-743.
- Caccianiga, M., Cerabolini, B., Luzzaro, A., De Bernardi, F., & Pierce, S. (2010) Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. *Community Ecology*, 11 (2): 223-231
- Gobbi, M., Rossaro, B., Vater, A., De Bernardi, F., Pelfini, M. & Brandmayr, P. (2007) Environmental features influencing Carabid beetle (Coleoptera) assemblages along a recently deglaciated area in the Alpine region. *Ecological Entomology*, 32: 282-289
- Gobbi, M., Isaia, M., & De Bernardi, F. (2011) Arthropod colonisation of a debris-covered glacier. *The Holocene*, 21 (2): 343-349
- Gobbi, M., Bragalanti, N., Lencioni, V. & Pedrotti, L. (2013) Contributo alla conoscenza delle comunità di carabidi (Coleoptera: Carabidae) del Parco Nazionale dello Stelvio (Settore Trentino). *Bollettino del Museo Civico di Storia Naturale di Verona*, 37:123-130.
- Gobbi, M., Fontaneto, D., Bragalanti, N., Pedrotti, L., & Lencioni, V. (2015) Carabid beetle (Coleoptera: Carabidae) richness and functional traits in relation to differently managed grasslands in the Alps. *Annales de la Société entomologique de France - International Journal of Entomology*: 51: 52-59.
- Maffioletti, M., Losapio, G., Tampucci, D., Isaia, M., Ballarin, F., Compostella, C., Seppi, R., & Caccianiga, M. (2017) Life in harsh environments: carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland. *Ecological Entomology*, 42(6): 838-848.
- Negro M., Isaia M., Palestini C. & Rolando A. (2009). The impact of forest ski-pistes on diversity of ground-dwelling arthropods and small mammals in the Alps. *Biodiversity & Conservation*. 18:2799-2821.
- Negro M., Isaia M., Palestini C., Schoenhofer A. & Rolando A. (2010). The impact of high-altitude ski pistes on ground-dwelling arthropods in the Alps. *Biodiversity & Conservation*. 19:1853-1870
- Negro M., Rolando A., Barni E., Bocola D., Filippa G., Freppaz M., Isaia M., Siniscalco C. & Palestini C. (2013a). Differential responses of ground dwelling arthropods to ski-piste restoration by hydroseeding. *Biodiversity & Conservation*. 22:2607-2634.
- Negro M., La Rocca C., Ronzani S., Rolando A. & Palestini C. (2013 b). Management tradeoffs between endangered species and biodiversity: the case of *Carabus olympiae* (Coleoptera: Carabidae) and carabid diversity in the western Italian Alps. *Biological Conservation*. 157: 255–265.
- Pizzolotto, R., Gobbi, M. & Brandmayr, P. (2014). Changes in ground beetle assemblages above and below the treeline of the Dolomites after almost 30 years (1980/2009). *Ecology & Evolution*, 4, 1284–1294.
- Tampucci, D., Azzoni, R.A., Marano, G., Boracchi, P., Citterio, C., Compostella, C., Diolaiuti, G., Isaia, M., Smiraglia, C., Gobbi, M., & Caccianiga, M. (2017) Debris-covered glaciers as habitat for plant and arthropod species: environmental framework and colonization patterns. *Ecological Complexity*, 32(Part A): 42-52

Appendix S2. Preliminary analyses and Principal Components Analysis of habitat

The potential effect of sampling effort on probability of carabid presence were assessed by defining exposure days x the number of traps per sampling site as a measure of effort. This variable was log-transformed, centred and standardized before analysis. A GLMM was then run, modelling species presence in relation to linear and quadratic effects of effort, specifying species as a random factor. There was a highly significant effect of both linear ($\chi^2 = 36.22$, $p > 0.0001$) and quadratic effort terms ($\chi^2 = 9.94$, $p > 0.001$), showing the probability of occurrence increased at an accelerating rate with an increase in effort (Fig. S1). Linear and quadratic effort terms were included in all subsequent models to account for this effect. There were 58 sites on ski pistes, all from W-Alps. A preliminary model (including effort, as above) found no evidence of a difference between the probability of carabid occurrence on ski pistes compared to other habitats within this region ($\chi^2 = 0.142$, $p = 0.71$), so these were included in subsequent analyses.

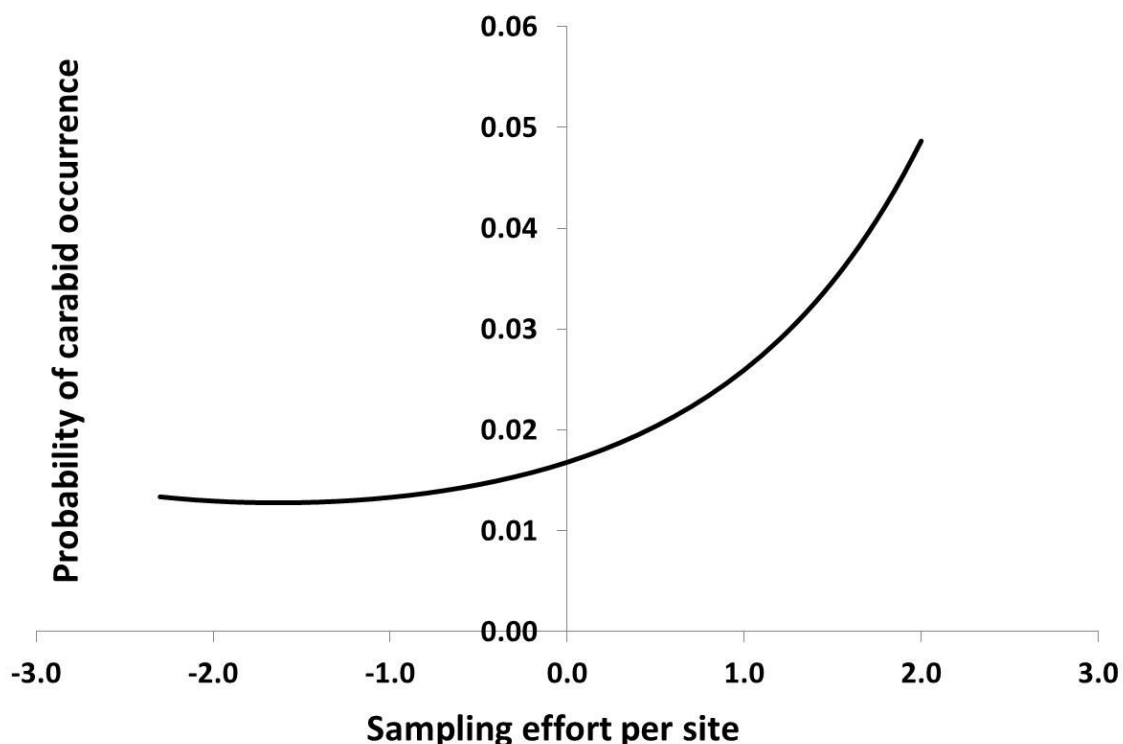


FIGURE S1. Fitted model of the effect of sampling effort per site (the product of the number of traps and the total exposure days, log-transformed, scaled and centred) on the probability of carabid presence combining data from all regions.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S2. Loadings for the first two axes of a Principal Components Analysis on the cover of different habitat types in 433 sites in the Italian Alps. Numbers in brackets are the percentage variation in the data explained by each axis. Black cells indicate loadings close to zero on each axis.

Habitat	Axis 1 (20%)	Axis 2 (17%)
Coniferous forest	0.767	0.357
Mixed forest		-0.470
Broad-leaved forest	-0.109	-0.501
Grass	-0.616	0.581
Shrubs		-0.125
Rocks	-0.133	-0.196
Unvegetated		

For Peer Review

Appendix S3. Details of models analysing carabid species presence in relation to traits, elevation and region.

Table S3. Model results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels.

(a) Body size and elevation (n = 72311 observations, 31 study areas, 167 species, AIC = 21111.1)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.978 \pm 0.125	-31.824	<0.001
Effort	0.257 \pm 0.055	4.621	<0.001
Effort ²	0.079 \pm 0.032	2.441	0.013
Elevation	-0.228 \pm 0.036	-6.255	<0.001
Elevation \times Size	-0.193 \pm 0.019	-10.140	<0.001

(b) Wing development and elevation (n = 72311 observations, 31 study areas, 167 species, AIC = 21174.7)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.967 \pm 0.125	-31.684	<0.001
Effort	0.252 \pm 0.055	4.552	<0.001
Effort ²	0.078 \pm 0.032	2.466	0.014
Elevation	-0.380 \pm 0.040	-9.517	<0.001
Elevation \times Wing(d)	0.242 \pm 0.052	4.654	<0.001
Elevation \times Wing(m)	0.280 \pm 0.048	5.863	<0.001

(c) Body size, elevation and region (n = 72311 observations, 31 study areas, 167 species, AIC = 21073.1)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.974 \pm 0.126	-31.519	<0.001
Effort	0.257 \pm 0.056	4.567	<0.001
Effort ²	0.079 \pm 0.032	2.463	0.014
Elevation	-0.237 \pm 0.037	-6.490	<0.001
Elevation \times Size	-0.033 \pm 0.032	-1.041	0.296
Size \times Region(E-Alps)	0.018 \pm 0.060	0.295	0.768
Size \times Region(W-Alps)	0.074 \pm 0.041	1.793	0.073
Elevation \times Size \times Region(E-Alps)	-0.194 \pm 0.074	-2.639	0.008
Elevation \times Size \times Region(W-Alps)	-0.241 \pm 0.041	-5.852	<0.001

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

(d) Body size and elevation, W-Alps (n = 44088 observations, 13 study areas, 167 species, AIC = 9843.9)

Explanatory variable	Estimate ± se	z	P
Intercept	-5.430 ± 0.259	-20.981	<0.001
Effort	0.422 ± 0.143	2.945	0.003
Effort ²	0.152 ± 0.105	1.452	0.146
Elevation	0.115 ± 0.085	1.351	0.177
Elevation×Size	-0.376 ± 0.031	-12.005	<0.001

(e) Body size and elevation, CE-Alps (n = 20875 observations, 15 study areas, 167 species, AIC = 6272.0)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.750 ± 0.215	-22.062	<0.001
Effort	0.242 ± 0.139	1.744	0.081
Effort ²	0.132 ± 0.069	1.906	0.057
Elevation	-0.448 ± 0.042	-10.567	<0.001
Elevation×Size	-0.028 ± 0.032	-0.895	0.370

(f) Body size and elevation, E-Alps (n = 7348 observations, 3 study areas, 167 species, AIC = 2310.3)

Explanatory variable	Estimate ± se	z	P
Intercept	-6.289 ± 0.842	-7.461	<0.001
Effort	-0.162 ± 0.141	-1.153	0.259
Effort ²	0.052 ± 0.115	0.453	0.642
Elevation	-0.046 ± 0.098	-0.469	0.657
Elevation×Size	-0.292 ± 0.079	-3.722	<0.001

(g) Wing development, elevation and region (n = 72311 observations, 31 study areas, 167 species, AIC = 20845.1)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.814 \pm 0.129	-29.658	<0.001
Effort	0.207 \pm 0.050	4.173	<0.001
Effort ²	0.086 \pm 0.029	2.982	0.003
Elevation	-0.238 \pm 0.057	-4.195	<0.001
Elevation \times Wings(d)	-0.440 \pm 0.084	-5.256	<0.001
Elevation \times Wings(m)	-0.308 \pm 0.077	-4.005	<0.001
Wingsb \times Region(E-Alps)	0.561 \pm 0.201	2.787	<0.001
Wingsd \times Region(E-Alps)	0.169 \pm 0.227	0.743	0.458
Wingsm \times Region(E-Alps)	-0.834 \pm 0.266	-3.134	0.002
Wingsb \times Region(WAlps)	-0.147 \pm 0.133	-1.109	0.268
Wingsd \times Region(WAlps)	-1.135 \pm 0.156	-7.290	<0.001
Wingsm \times Region(WAlps)	-0.535 \pm 0.144	-3.714	0.238
Elevation \times Wings(b) \times Region(E-Alps)	0.137 \pm 0.116	1.181	<0.001
Elevation \times Wings(d) \times Region(E-Alps)	0.672 \pm 0.182	3.692	<0.001
Elevation \times Wings(m) \times Region(E-Alps)	1.169 \pm 0.300	3.900	<0.001
Elevation \times Wings(b) \times Region(WAlps)	-0.056 \pm 0.094	-0.598	0.550
Elevation \times Wings(d) \times Region(WAlps)	1.108 \pm 0.125	8.891	<0.001
Elevation \times Wings(m) \times Region(WAlps)	0.958 \pm 0.111	8.651	<0.001

(h) Wing development and elevation, W-Alps (n = 44088 observations, 13 study areas, 167 species, AIC = 9830.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-5.427 \pm 0.257	-21.105	<0.001
Effort	0.422 \pm 0.142	2.982	0.003
Effort ²	0.155 \pm 0.103	1.505	0.132
Elevation	-0.278 \pm 0.087	-3.215	0.001
Elevation \times Wing(d)	0.791 \pm 0.082	9.844	<0.001
Elevation \times Wing(m)	0.766 \pm 0.067	11.427	<0.001

(i) Wing development and elevation, CE-Alps (n = 20875 observations, 15 study areas, 167 species, AIC = 6254.7)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.766 \pm 0.214	-22.213	<0.001
Effort	0.275 \pm 0.141	1.947	0.052
Effort ²	0.119 \pm 0.070	1.698	0.090
Elevation	-0.276 \pm 0.058	-4.731	<0.001
Elevation \times Wing(d)	-0.358 \pm 0.088	-4.085	<0.001
Elevation \times Wing(m)	-0.270 \pm 0.084	-3.223	<0.001

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

(j) Wing development and elevation, E-Alps (n = 7348 observations, 3 study areas, 167 species, AIC = 2322.0)

Explanatory variable	Estimate ± se	z	P
Intercept	-6.242 ± 0.908	-7.079	<0.001
Effort	-0.161 ± 0.140	-1.150	0.250
Effort ²	0.053 ± 0.115	0.463	0.643
Elevation	-0.186 ± 0.115	-1.622	0.105
Elevation×Wing(d)	0.112 ± 0.203	0.549	0.583
Elevation×Wing(m)	0.589 ± 0.291	2.027	0.043

For Peer Review

Appendix S4. Variograms based on residuals from elevation×body size and elevation×body size×region models. Note variograms were very similar when considering residuals from wing development models.

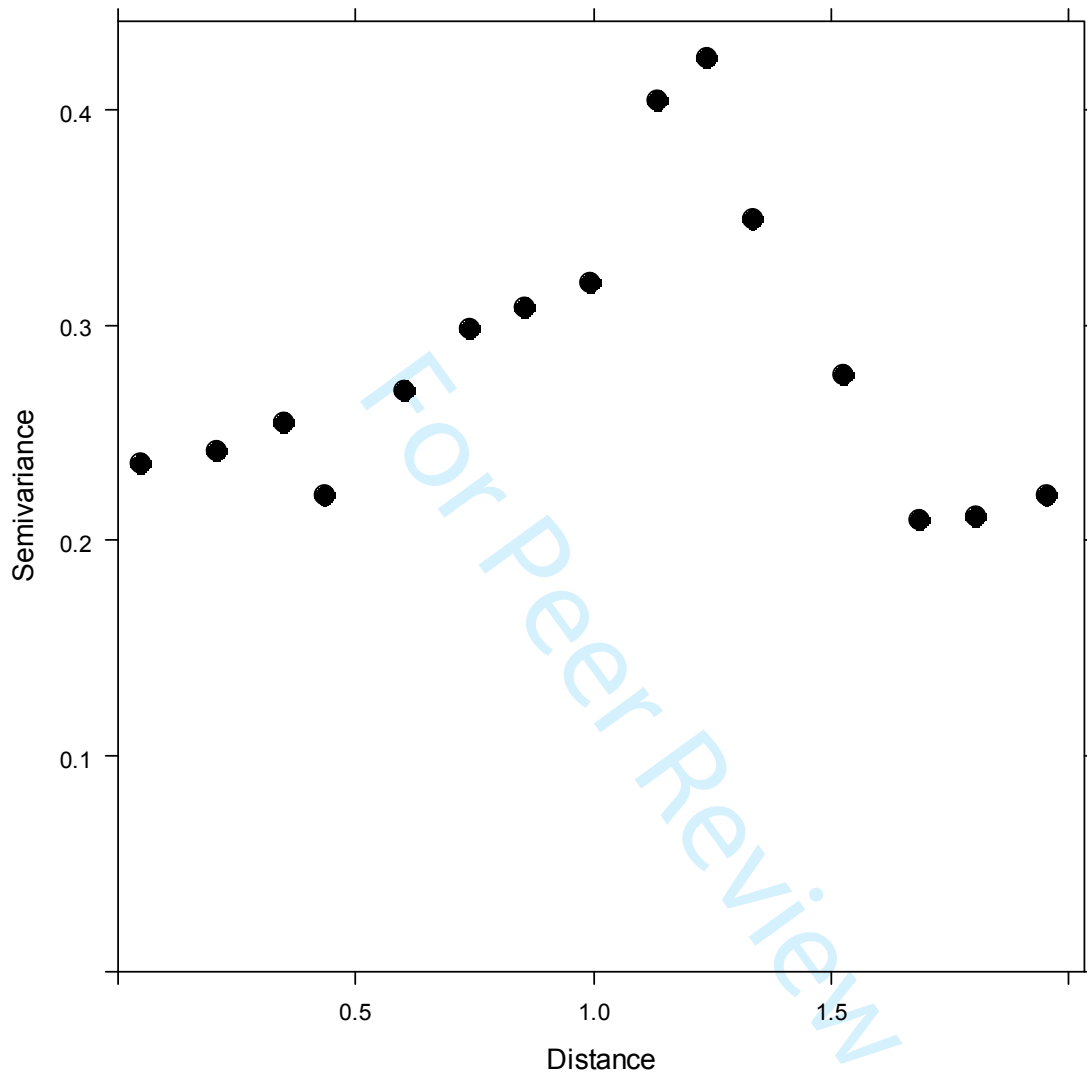


Fig. S2. Variogram of model residuals from Fig. 2.

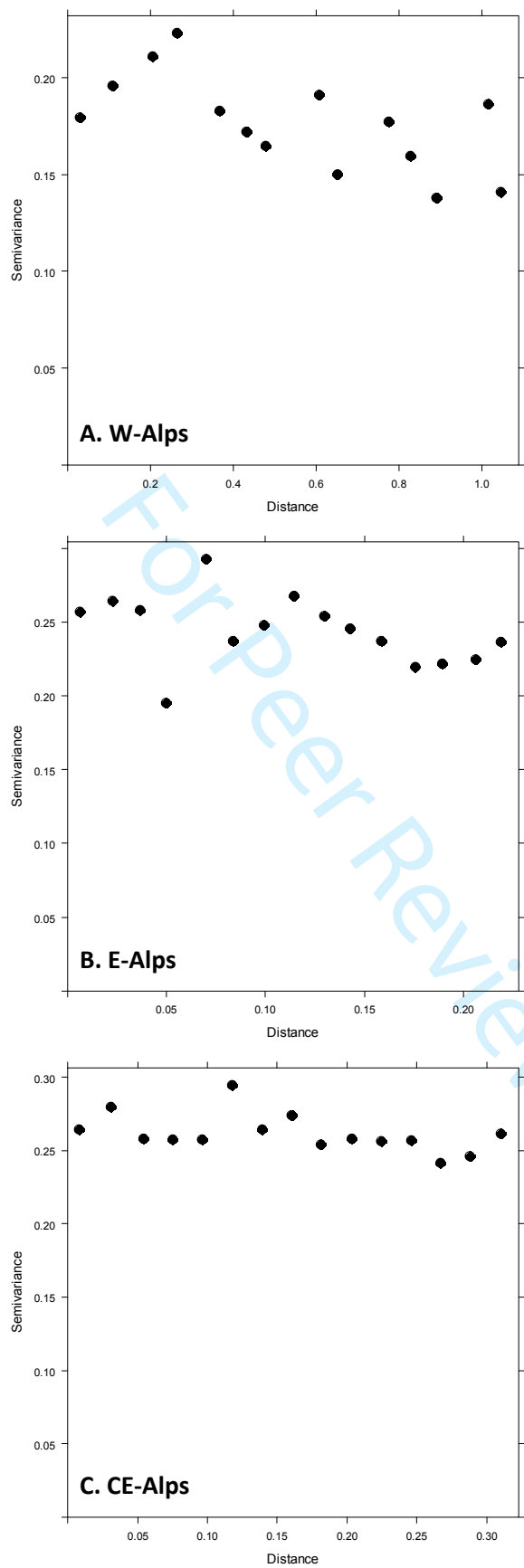


Fig. S3. Variogram of model residuals from Fig. 3.

Appendix S5. Details of models analysing carabid species presence in relation to traits and elevation considering only relatively common species (at least 20 occurrences in the data set).

Table S4. Results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels.

(a) Body size (n = 21217 observations, 31 study areas, 49 species, AIC = 13469.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-2.525 \pm 0.138	-18.309	<0.001
Effort	0.223 \pm 0.069	3.240	0.0012
Effort ²	0.074 \pm 0.039	1.893	0.0584
Elevation	-0.246 \pm 0.043	-5.667	<0.001
Elevation \times Size	-0.205 \pm 0.024	-8.557	<0.001

(b) Wing development (n = 21217 observations, 31 study areas, 49 species, AIC = 13456.7)

Explanatory variable	Estimate \pm se	z	P
Intercept	-2.523 \pm 0.137	-18.411	<0.001
Effort	0.224 \pm 0.069	3.256	0.001
Effort ²	0.075 \pm 0.039	1.899	0.058
Elevation	-0.407 \pm 0.047	-8.666	<0.001
Elevation \times Wing(d)	0.513 \pm 0.060	8.611	<0.001
Elevation \times Wing(m)	0.368 \pm 0.062	5.937	<0.001

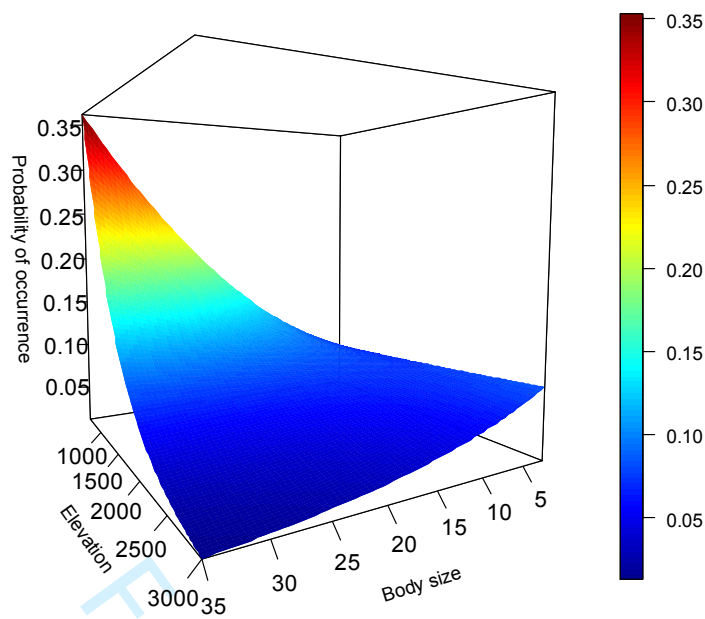


Fig. S4. Probability of carabid presence in relation to elevation and body size, considering only species with at least 20 occurrences in the whole sample.

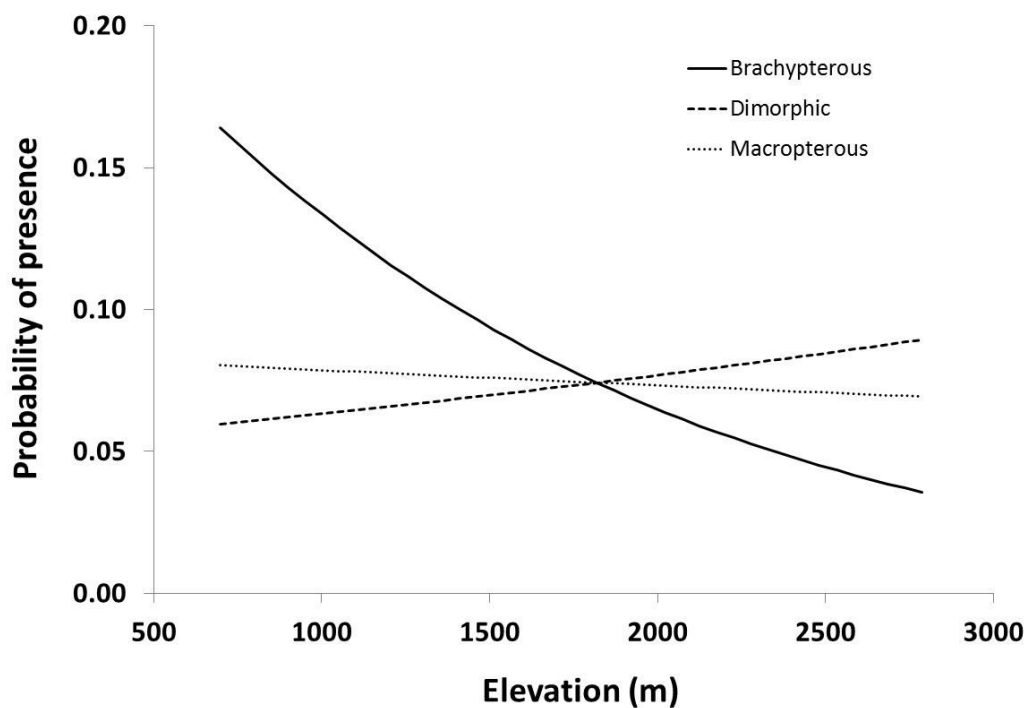


Fig. S5. Probability of carabid presence in relation to elevation and wing development, considering only species with at least 20 occurrences in the whole sample.

Appendix S6. Details of models analysing carabid species presence in relation to traits, elevation and region omitting sites (n = 17) from the Maritime Alps (part of the W-Alps region).

Table S5. Results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels.

(a) Body size and elevation (n = 69472 observations, 28 study areas, 167 species, AIC = 19857.6)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.066 \pm 0.137	-29.746	<0.001
Effort	0.263 \pm 0.058	4.513	<0.001
Effort ²	0.082 \pm 0.033	2.520	0.012
Elevation	-0.227 \pm 0.037	-6.163	<0.001
Elevation \times Size	-0.196 \pm 0.019	-10.224	<0.001

(b) Wing development and elevation (n = 69472 observations, 28 study areas, 167 species, AIC = 19922.4)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.054 \pm 0.137	-29.689	<0.001
Effort	0.259 \pm 0.058	4.438	<0.001
Effort ²	0.081 \pm 0.033	2.500	0.012
Elevation	-0.379 \pm 0.040	-9.377	<0.001
Elevation \times Wing(d)	0.245 \pm 0.052	4.738	<0.001
Elevation \times Wing(m)	0.289 \pm 0.048	5.911	<0.001

(c) Body size, elevation and region (n = 69472 observations, 28 study areas, 167 species, AIC = 19821.9)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.063 \pm 0.138	-29.496	<0.001
Effort	0.263 \pm 0.059	4.461	<0.001
Effort ²	0.083 \pm 0.033	2.502	0.012
Elevation	-0.236 \pm 0.037	-6.361	<0.001
Elevation \times Size	-0.034 \pm 0.032	-1.077	0.281
Size \times Region(E-Alps)	0.013 \pm 0.060	0.225	0.822
Size \times Region(W-Alps)	0.035 \pm 0.043	0.804	0.421
Elevation \times Size \times Region(E-Alps)	-0.195 \pm 0.074	-2.647	0.008
Elevation \times Size \times Region(W-Alps)	-0.253 \pm 0.042	-6.094	<0.001

(d) Body size and elevation, W-Alps (n = 41249 observations, 10 study areas, 167 species, AIC = 8456.7)

Explanatory variable	Estimate \pm se	z	P
Intercept	-5.932 \pm 0.334	-17.757	<0.001
Effort	0.399 \pm 0.418	0.956	0.339
Effort ²	0.110 \pm 0.246	0.448	0.654
Elevation	0.146 \pm 0.094	1.557	0.120
Elevation \times Size	-0.407 \pm 0.033	-12.177	<0.001

(e) Wing development, elevation and region (n = 69472 observations, 28 study areas, 167 species, AIC = 19592.4)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.883 \pm 0.138	-28.072	<0.001
Effort	0.171 \pm 0.055	3.094	0.002
Effort ²	0.092 \pm 0.030	3.115	0.002
Elevation	-0.249 \pm 0.057	-4.341	<0.001
Elevation \times Wings(d)	-0.434 \pm 0.084	-5.186	<0.001
Elevation \times Wings(m)	-0.310 \pm 0.077	-4.011	<0.001
Wingsb \times Region(E-Alps)	0.549 \pm 0.214	2.569	0.010
Wingsd \times Region(E-Alps)	0.151 \pm 0.238	0.636	0.525
Wingsm \times Region(E-Alps)	-0.848 \pm 0.276	-3.074	0.002
Wingsb \times Region(WAlps)	-0.269 \pm 0.159	-1.687	0.092
Wingsd \times Region(WAlps)	-1.267 \pm 0.180	-7.054	<0.001
Wingsm \times Region(WAlps)	-0.725 \pm 0.170	-4.264	<0.001
Elevation \times Wings(b) \times Region(E-Alps)	0.135 \pm 0.117	1.154	0.249
Elevation \times Wings(d) \times Region(E-Alps)	0.665 \pm 0.182	3.646	<0.001
Elevation \times Wings(m) \times Region(E-Alps)	1.174 \pm 0.302	3.888	<0.001
Elevation \times Wings(b) \times Region(WAlps)	-0.001 \pm 0.097	-0.013	0.990
Elevation \times Wings(d) \times Region(WAlps)	1.159 \pm 0.127	9.128	<0.001
Elevation \times Wings(m) \times Region(WAlps)	1.033 \pm 0.114	9.023	<0.001

(f) Wing development and elevation, W-Alps (n = 41249 observations, 10 study areas, 167 species, AIC = 8544.0)

Explanatory variable	Estimate \pm se	z	P
Intercept	-5.913 \pm 0.331	-17.881	<0.001
Effort	0.934 \pm 0.411	0.959	0.338
Effort ²	0.111 \pm 0.242	0.461	0.645
Elevation	-0.246 \pm 0.095	-2.579	0.010
Elevation \times Wing(d)	0.805 \pm 0.084	9.572	<0.001
Elevation \times Wing(m)	0.795 \pm 0.071	11.234	<0.001

Appendix S7 Details of models analysing carabid species presence in relation to traits, habitat and region.

Table S6. Results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels. Habitat was defined according to two PCA axes (Axis1 and Axis2, defined in Table 2).

(a) Body size and Axis1 (n = 72311 observations, 31 study areas, 167 species, AIC = 21266.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.069 \pm 0.132	-30.930	<0.001
Effort	0.341 \pm 0.057	6.028	<0.001
Effort ²	0.104 \pm 0.033	3.146	0.002
Axis1	-0.022 \pm 0.017	-1.321	0.186
Axis1 \times Size	0.003 \pm 0.015	0.175	0.861

(b) Body size and Axis2 (n = 72311 observations, 31 study areas, 167 species, AIC = 21268.0)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.096 \pm 0.132	-30.940	<0.001
Effort	0.340 \pm 0.057	6.017	<0.001
Effort ²	0.104 \pm 0.033	3.157	0.002
Axis2	-0.003 \pm 0.018	-0.188	0.851
Axis2 \times Size	0.008 \pm 0.016	0.507	0.612

(c) Wing development and Axis1 (n = 72311 observations, 31 study areas, 167 species, AIC = 21267.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.070 \pm 0.132	-30.936	<0.001
Effort	0.341 \pm 0.057	6.032	<0.001
Effort ²	0.104 \pm 0.033	3.144	0.002
Axis1	-0.022 \pm 0.022	-1.000	0.317
Axis1 \times Wing(d)	0.030 \pm 0.043	0.681	0.500
Axis1 \times Wing(m)	-0.023 \pm 0.040	-0.565	0.572

(d) Wing development and Axis2 (n = 72311 observations, 31 study areas, 167 species, AIC = 21268.9)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.069 ± 0.132	-30.937	<0.001
Effort	0.340 ± 0.056	6.016	<0.001
Effort ²	0.104 ± 0.033	3.153	0.002
Axis2	0.016 ± 0.023	0.698	0.485
Axis2×Wing(d)	-0.045 ± 0.046	-0.970	0.332
Axis2×Wing(m)	-0.039 ± 0.042	-0.917	0.359

(e) Body size, Axis1 and region (n = 72311 observations, 31 study areas, 167 species, AIC = 21247.5)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.070 ± 0.132	-30.934	<0.001
Effort	0.343 ± 0.057	6.020	<0.001
Effort ²	0.102 ± 0.033	3.075	0.002
Axis1	-0.023 ± 0.017	-1.355	0.175
Axis1×Size	0.008 ± 0.027	0.301	0.764
Size×Region(E-Alps)	-0.004 ± 0.059	-0.061	0.951
Size×Region(W-Alps)	0.181 ± 0.039	4.707	<0.001
Axis1×Size×Region(E-Alps)	-0.040 ± 0.050	-0.807	0.420
Axis1×Size×Region(W-Alps)	0.002 ± 0.033	0.062	0.950

(f) Body size, Axis2 and region (n = 72311 observations, 31 study areas, 167 species, AIC = 21249.6)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.070 ± 0.132	-30.930	<0.001
Effort	0.343 ± 0.057	6.010	<0.001
Effort ²	0.102 ± 0.033	3.082	0.002
Axis2	-0.003 ± 0.018	-0.175	0.861
Axis2×Size	-0.001 ± 0.028	-0.049	0.961
Size×Region(E-Alps)	-0.005 ± 0.059	-0.081	0.935
Size×Region(W-Alps)	0.181 ± 0.039	4.703	<0.001
Axis2×Size×Region(E-Alps)	0.018 ± 0.055	0.334	0.738
Axis2×Size×Region(W-Alps)	0.014 ± 0.035	0.408	0.683

(g) Wing development, Axis1 and region (n = 69472 observations, 28 study areas, 167 species, AIC = 21116.3)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.909 \pm 0.145	-26.911	<0.001
Effort	0.304 \pm 0.055	5.508	<0.001
Effort ²	0.119 \pm 0.033	3.700	<0.001
Axis1	-0.001 \pm 0.040	-0.010	0.992
Axis1×Wings(d)	0.058 \pm 0.070	0.836	0.403
Axis1×Wings(m)	0.004 \pm 0.065	0.061	0.951
Wingsb×Region(E-Alps)	0.516 \pm 0.265	1.927	0.054
Wingsd×Region(E-Alps)	0.121 \pm 0.283	0.427	0.670
Wingsm×Region(E-Alps)	-0.709 \pm 0.295	-2.405	0.016
Wingsb×Region(WAlps)	0.006 \pm 0.165	0.033	0.973
Wingsd×Region(WAlps)	-1.159 \pm 0.184	-6.316	<0.001
Wingsm×Region(WAlps)	-0.583 \pm 0.175	-3.337	<0.001
Axis1×Wings(b)×Region(E-Alps)	-0.132 \pm 0.071	-1.865	0.062
Axis1×Wings(d)×Region(E-Alps)	-0.071 \pm 0.111	-0.637	0.524
Axis1×Wings(m)×Region(E-Alps)	0.106 \pm 0.126	0.835	0.404
Axis1×Wings(b)×Region(WAlps)	-0.004 \pm 0.050	-0.080	0.936
Axis1×Wings(d)×Region(WAlps)	-0.114 \pm 0.085	-1.347	0.178
Axis1×Wings(m)×Region(WAlps)	-0.118 \pm 0.071	-1.654	0.098

(h) Wing development, Axis2 and region (n = 69472 observations, 28 study areas, 167 species, AIC = 21125.6)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.911 \pm 0.145	-26.954	<0.001
Effort	0.306 \pm 0.055	5.546	<0.001
Effort ²	0.119 \pm 0.032	3.698	<0.001
Axis2	0.014 \pm 0.043	0.338	0.735
Axis2×Wings(d)	-0.047 \pm 0.075	-0.617	0.537
Axis2×Wings(m)	-0.062 \pm 0.069	-0.904	0.366
Wingsb×Region(E-Alps)	0.516 \pm 0.264	1.953	0.051
Wingsd×Region(E-Alps)	0.117 \pm 0.282	0.416	0.678
Wingsm×Region(E-Alps)	-0.696 \pm 0.294	-2.369	0.018
Wingsb×Region(WAlps)	0.007 \pm 0.164	0.042	0.966
Wingsd×Region(WAlps)	-1.164 \pm 0.183	-6.356	<0.001
Wingsm×Region(WAlps)	-0.570 \pm 0.174	-3.274	0.001
Axis2×Wings(b)×Region(E-Alps)	-0.004 \pm 0.075	-0.054	0.957
Axis2×Wings(d)×Region(E-Alps)	0.127 \pm 0.121	1.050	0.294
Axis2×Wings(m)×Region(E-Alps)	0.037 \pm 0.140	0.264	0.792
Axis2×Wings(b)×Region(WAlps)	0.003 \pm 0.052	0.060	0.952
Axis2×Wings(d)×Region(WAlps)	-0.051 \pm 0.090	-0.574	0.566
Axis2×Wings(m)×Region(WAlps)	0.055 \pm 0.074	0.735	0.463